# ASPECTS OF GENETIC RELATIONSHIPS AND VARIATION IN PARROTS OF THE CRIMSON ROSELLA *PLATYCERCUS ELEGANS* COMPLEX (AVES: PSITTACIDAE)

by Leo Joseph & Rory Hope*

**Summary**

Joseph, L. & Hope, R. (1984). Aspects of genetic relationships and variation in the parrots of the Crimson Rosella *Platycercus elegans* complex (Aves: Psittacidae). *Trans. R. Soc. S. Aust.* **108**(2), 77-84, 12 June, 1984.

Enzyme electrophoresis was used to examine genetic variation within and between three of the four principal parrot taxa of the Crimson Rosella *Platycercus elegans* complex of eastern Australia. Comparisons were made with the results of recent studies of other birds, mainly Northern Hemisphere members of the Order Passeriformes in which it has been shown that although populations of birds show levels of variation in isozymes comparable with those in other vertebrates, levels of isozymic differentiation and thus structural gene differentiation between bird taxa are unusually low. The data from rosellas, which belong to the Order Psittaciformes, although necessarily limited and therefore somewhat equivocal with respect to these generalizations, appear to be consistent with them, especially the former. No significant or consistent geographical patterns of gene frequency differences were detected among the rosellas studied.

Key Words: Birds, electrophoresis, population genetics, *Platycercus elegans*.

## Introduction

Four principal parrot taxa comprise the Crimson Rosella *Platycercus elegans* complex in eastern Australia (see Fig. 1a and Forshaw 1981, for details of habitat and distribution). One, the Crimson Rosella *P. elegans*, ranges south from the Atherton Tableland, Queensland, along Australia's eastern coast to south-eastern South Australia with an isolated population on Kangaroo Island. Adults are predominantly crimson, immatures green. A second, the Yellow Rosella *P. flaveolus*, is confined to the Murray-Darling river system. In general, the crimson in the plumage of *P. elegans* is replaced by yellow in this form. In the Mt Lofty Ranges and southern Flinders Ranges there occurs a third form, a series of populations all of which are variable in colour but intermediate between *P. elegans* and *P. flaveolus*. These are collectively termed here the Adelaide Rosella *P. adelaidae*. There is clinal variation in plumage in *P. adelaidae*, particularly on the ventral surface (Forshaw 1981). In the southern Mt Lofty Ranges adults are, generally, rich scarlet. Northwards, they become progressively lighter and more orange. Populations in the Flinders Ranges are predominantly yellow ventrally but usually have a strong wash of orange. The fourth member of the complex, the Green Rosella *P. caledonicus* of Tasmania and the larger Bass Strait islands, was not included in this study.

There has been considerable debate over the relationships and taxonomic status of these parrots. Condon (1954) proposed that *P. adelaidae* evolved through hybridization between *P. elegans* and *P. flaveolus*. This is suggested by the intermediate colouration of *P. adelaidae* (see also Martindale 1974[1], Forshaw 1981). Also, the south-north cline in colouration of *P. adelaidae* is most simply explained perhaps as having arisen through introgression of *P. flaveolus* genes from the north and *P. elegans* genes from the south. If so, this would afford further support for some previous hybridization. Cain (1955) and Keast (1961), on the other hand, suggested that the members of the complex evolved *in situ* in response to climatic changes.

Two generalizations have emerged from recent electrophoretic studies of genic variation in birds. Firstly, populations of birds do not differ significantly from those of other vertebrates in levels of within-population variation. Secondly, there seems to be considerably less genic differentiation between bird taxa than

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[1] Martindale, J. (1974). Some ecogenetic relationships and their origins in platycercine species complex (Order Psittaciformes, Class Aves) of south-eastern Australia. Honours Thesis, Department of Genetics and Human Variation, La Trobe University, Victoria. Unpubl.

between taxa of other vertebrate classes at equivalent levels of the taxonomic hierarchy (see, for example, Avise & Aquadro 1982 and references therein and an alternative view offered by Sibley & Ahlquist 1982).

These generalizations have grown largely out of studies of passerine birds. Concerning Australian species, data are at present available only for the Grey-crowned Babbler *Pomatostomus temporalis*, a communally breeding passerine, and from some species of the passerine family Hirundinidae (Johnson & Brown, 1980; Manwell & Baker, 1975). Thus, the present study of non-passerine birds aimed (1) to measure levels of electrophoretically detectable genic variation between and within some members of the Crimson Rosella complex, and (2) to compare them with such levels measured in other birds and vertebrates in general.

## Materials and Methods

Collecting Procedures: Specimens of rosellas were collected under a permit from the South Australian National Parks and Wildlife Service. Within an hour of death, samples of liver, heart muscle and breast muscle were extracted for electrophoresis and transported in dry ice to the laboratory where they were stored at −20° C. Specimens were sexed by dissection and aged as adult or immature from plumage (Lendon 1973). Stomach contents have been preserved and the birds have been prepared as voucher study skins and lodged in the South Australian Museum, Adelaide. The collecting localities are shown in Fig. 1b.

Adelaide Rosella *P. adelaidae*: 59 specimens were collected to sample *P. adelaidae* as evenly as feasible throughout its range. They were collected in six geographical sectors: S, extreme southern Mt Lofty Ranges =

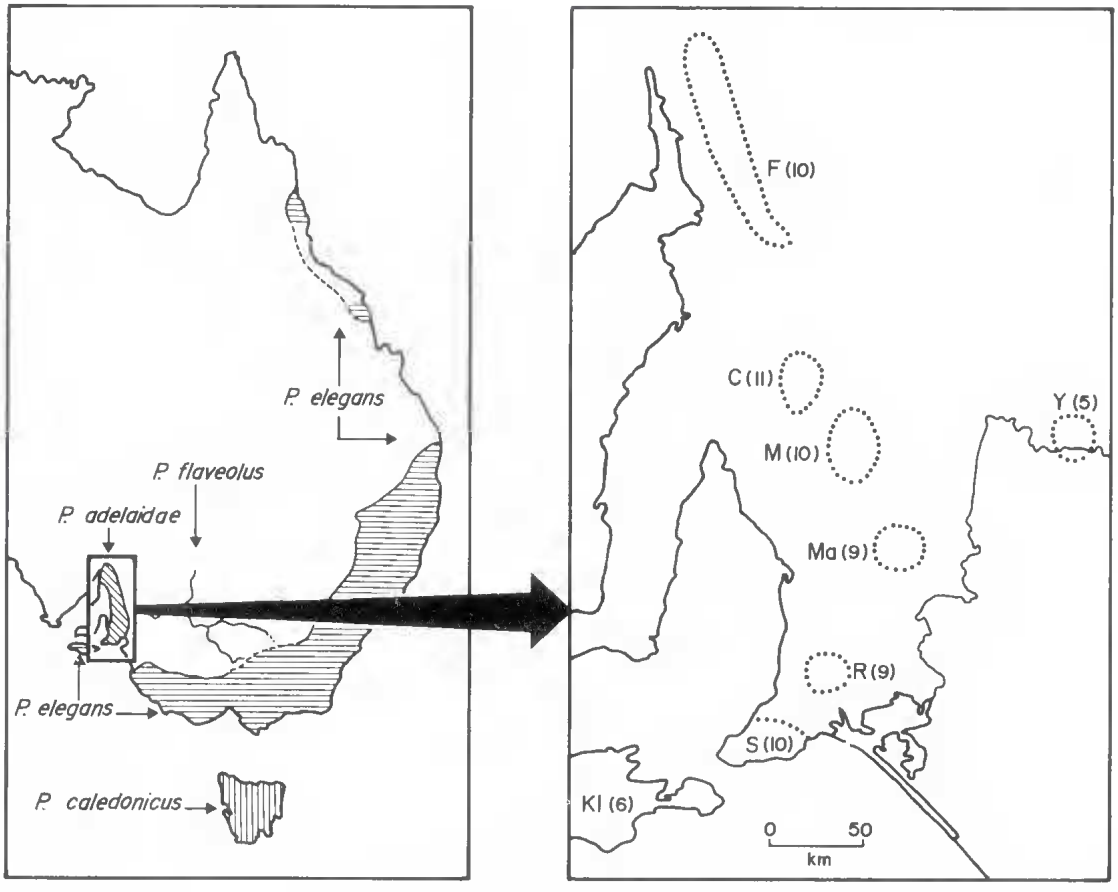


Fig. 1. (a) Approximate distribution of members of the *P. elegans* complex in eastern Australia. (b) Localities and sample sizes collected for this study; letters are the abbreviated names of each sample.

Fleurieu Peninsula (10 specimens); R, southern central Mt Lofty Ranges between Ashbourne and Meadows (9); Ma, lower Marne River and environs (9); M, northern central Mt Lofty Ranges between Kapunda and Saddleworth (10); C, northern Mt Lofty Ranges between Auburn and Clare (11); and F, southern Flinders Ranges between Jamestown and the Dutchman's Stern (10). No more than three specimens were taken from one locality within these sectors with the exceptions of 15 km NE of Saddleworth and the Dutchman's Stern. Sample F was taken over a larger area than the other samples because of the logistic difficulties involved in sampling the Flinders Ranges birds and because it was intended to treat these birds as a distinct sub-population of *P. adelaidae* in subsequent data analyses.

Crimson Rosella *P. elegans*: six specimens were taken from four localities at the western end of Kangaroo Island. In addition, the livers of four from the South-East of S.A. and of six from the Atherton Tableland, Qld were examined. Voucher specimens of the latter two samples are held in the Australian National Wildlife Collection, Canberra.

Yellow Rosella *P. flaveolus*: five specimens from near the Murray River between Barmera and Waikerie were examined.

Other species: organ extracts were obtained from the parrot genera *Barnardius* and *Psephotus*, both of which are closely related to *Platycercus* (Cain 1955) and of a more distantly related bird, a pigeon. Details of these are as follows: the exotic Spotted Turtle-Dove *Streptopelia chinensis* (one individual, liver only, collected in grounds of University of Adelaide), Mallee Ringneck Parrot *Barnardius barnardi* (two, liver and heart muscle, near Swan Reach), Mulga Parrot *Psephotus varius* (one, liver and heart muscle, near Swan Reach), Red-rumped Parrot *Psephotus haematonotus* (one, liver only, near Mannum). The availability of these samples made possible genetic comparisons between the members of the *P. elegans* complex and other species.

Electrophoresis: Electrophoresis was carried out on cellulose acetate gels (Meera Khan 1971) following procedures of Baverstock *et al.* (1977). When electrophoresis revealed two forms of an enzyme (manifest as distinct sets of bands), the presumptive locus encoding the most anodal form was designated 1 and the other 2 e.g. *Idh–1*, *Idh–2* for isocitrate dehydrogenase. The presumptive allele encoding the most anodally migrating product of a locus was designated *a*, the second most anodal *b* and so on. In one case, *Pgd, b'* indicates an allelic form of the enzyme intermediate in mobility between $Pgd^b$ and $Pgd^c$.

Table 1 shows the enzymes assayed and the organ and electrophoresis buffer used for each enzyme. In all, nine enzymes were electrophoresed and choice of these was not entirely random, being determined partly by which enzymes were under investigation in the laboratory for other projects. Aconitase was examined to test a hypothesis of sex-linkage in birds (see Baverstock *et al.* 1982).

The symbols used to represent the locus or loci corresponding with each enzyme are: 6-phosphogluconate dehydrogenase, *Pgd*; purine nucleoside phosphorylase, *NP*; adenylate kinase, *Ak–1*, *Ak–2*; phosphoglucomutase, *Pgm*; isocitrate dehydrogenase, *Idh–1*, *Idh–2*;

TABLE 1. *Enzymes assayed and buffers and organs used for electrophoresis.*

| Enzyme | Buffer[1] | Organ[2] |
|---|---|---|
| 6-Phosphogluconate dehydrogenase | B + NADP | L |
| Purine nucleoside phosphorylase | A | L |
| Pyruvate kinase | C | L, H |
| Adenylate kinase | B | L |
| Phosphoglucomutase | C | L |
| Isocitrate dehydrogenase | B + NADP | L, H |
| Aconitase | B | L, H |
| Glucose phosphate isomerase | B | L |
| Glutamate oxaloacetate transaminase | B | L |

[1] Buffer code: A—0.01 M citrate-phosphate, pH 6.4; B—0.02 M phosphate, pH 7.0; C—0.05 M tris-maleate, pH 7.8; D—0.12 M tris-glycine, pH 9.5.

[2] Organ code: L—liver; H—heart.

+ NADP indicates that 600 µl of NADP (10 mg/ml) were added to the buffer placed in the cathodal compartment and in which the gel was soaked.

aconitase, *Acon–1*, *Acon–2*; glucose phosphate isomerase, *Gpi*, glutamate oxaloacetate transaminase, *Got* and pyruvate kinase, *Pk*.

Analysis of data: The proportion of polymorphic loci, P, was calculated directly using two definitions of polymorphism: one where the most common allele had a frequency of less than 0.99 and the other where this frequency was less than 0.95.

The average heterozygosity per locus, H (see Nei 1978), was calculated as:

$$H = \frac{\Sigma h}{r}$$

where r is the number of loci scored, and h is the expected heterozygosity at each locus, calculated as $1 - x_i$ where $x_i$ is the frequency of the ith allele at each locus.

Standard errors of H estimates have been discussed by Nei (1978) and Nei & Roychoudhury (1974), who concluded that it is more important when estimating H to screen many loci in few individuals rather than the converse. Gene frequencies were compared with t-tests and Fisher's exact method. So that comparisons could be made between *P. elegans* or *P. flaveolus* on one hand and *P. adelaidae* on the other, the *P. adelaidae* data for each locus were pooled, their homogeneity first being assessed by the method of Hancock (1975). Heterogeneity was detected only for the data from pyruvate kinase, which were accordingly not used in such data analyses.

## Results

### Electrophoretic Typings and Isozymic Variation within *P. adelaidae*

Tables 2 and 3 present the results of electrophoresis and Table 4 presents measures of genic variation within the rosellas and in vertebrates in general. The standard errors of the rosella H estimates are relatively large, e.g. approximately 0.05 for the H estimate of 0.104 in *P. adelaidae* (see Nei 1978). The estimates are, therefore, only coarse approximations. The data for *Pgd*, *Np*, and *Idh–2*, the most variable loci, showed *P. adelaidae* to

TABLE 2. *Numbers of individuals of indicated genotypes in population samples of the* P. elegans *complex. In samples of* P. elegans *itself, KI = Kangaroo Island, SE = South-East of South Australia, and A = Atherton Tableland, Qld. For brevity, genotypes are represented thus: at an indicated locus e.g.* Pgd, *a/a designates* $Pgd^a/Pgd^a$. *Wholly invariant loci are omitted. Heart samples for typing of* Acon–2 *and* Idh–2 *not available for samples SE and A.*

| Genotype | | *P. elegans* KI | *P. elegans* SE | *P. elegans* A | *P. adelaide* | *P. flaveolus* |
|---|---|---|---|---|---|---|
| Pgd | *a/a* | 2 | | | | |
| | *a/b* | | 1 | | 10 | 2 |
| | *b/b* | 4 | 2 | 5 | 39 | 2 |
| | *b'/c* | | | | 1 | |
| | *b/c* | | 1 | | 8 | 1 |
| | *c/c* | | | | 1 | |
| Np | *a/a* | 5 | 1 | – | 29 | 2 |
| | *a/b* | | 3 | | 23 | 2 |
| | *b/b* | | | | 5 | 1 |
| | *a/c* | | | | 2 | |
| Ak–1 | *a/b* | | | | 1 | |
| | *b/b* | 6 | 4 | 6 | 58 | 5 |
| Ak–2 | *a/b* | 1 | 1 | | | |
| | *b/b* | 5 | 3 | 6 | 59 | 5 |
| Pgm | *a/b* | | | | 1 | |
| | *b/b* | 6 | 4 | 6 | 58 | 5 |
| Idh–1 | *a/a* | | | 1 | | |
| | *a/b* | | | 2 | | |
| | *b/b* | 6 | 4 | 0 | 59 | 5 |
| Idh–2 | *b/b* | | | | 5 | |
| | *a/c* | | | | 2 | |
| | *a/b* | | | | 1 | 1 |
| | *a/a* | 6 | | | 48 | 4 |
| Acon–1 | *a/a* | | | | 1 | |
| | *b/b* | 5 | | | 57 | 5 |

TABLE 3. *Numbers of individuals of indicated genotypes in population samples of* P. adelaidae *designated S, R, Ma, M, C and F (see text). Genotypic symbolism as for Table 2. Wholly invariant loci are omitted.*

| Genotype | | Sample S | R | Ma | M | C | F |
|---|---|---|---|---|---|---|---|
| Pgd | *a/b* | | 3 | | 4 | 2 | 1 |
| | *b/b* | 8 | 5 | 6 | 5 | 6 | 9 |
| | b'/c | | 1 | | | | |
| | *b/c* | 2 | | 3 | 1 | 2 | |
| | *c/c* | | | | | 1 | |
| Np | *a/a* | 6 | 6 | 3 | 6 | 1 | 8 |
| | *a/b* | 2 | 3 | 5 | 3 | 8 | 2 |
| | *b/b* | 2 | | 1 | | 1 | |
| | *a/c* | | | | 1 | 1 | |
| Ak-1 | *a/b* | | | | 1 | | |
| | *b/b* | 10 | 9 | 9 | 9 | 11 | 10 |
| Pgm | *a/b* | | | | | | 1 |
| | *b/b* | 10 | 9 | 9 | 10 | 11 | 9 |
| Idh-2 | *c/a* | | | 2 | | | |
| | *b/c* | | | 1 | | | |
| | *c/c* | 7 | 7 | 6 | 10 | 8 | 10 |

TABLE 4. *Values of P, the proportion of polymorphic loci, and H, the average heterozygosity per locus, obtained in the* P. elegans *complex. Values for Vertebrata and Aves are from Nevo (1978).*

| Taxon | Loci scored | P Freq. of most common allele <0.99 | <0.95 | H |
|---|---|---|---|---|
| *P. adelaidae* | 10 | 0.3 | 0.3 | 0.104 |
| *P. elegans* | | | | |
| Kangaroo Island | 11 | 0.18 | 0.18 | 0.07 |
| South-East | 8 | 0.375 | 0.375 | 0.137 |
| Atherton Tableland | 8 | 0.125 | 0.125 | 0.05 |
| *P. flaveolus* | 11 | 0.27 | 0.27 | 0.102 |
| Vertebrata | — | 0.173 ± 0.119 | | 0.0494 ±0.0365 |
| Aves | — | 0.150 ± 0.111 | | 0.0473 ±0.0360 |

be in Hardy-Weinberg equilibrium (*Pgd*, $x^2_9 = 0.74$, $0.7>P>0.5$; *Np*, $x^2_1 = 0.025$, $0.9>P>0.8$; *Idh–2*, $x^2_2 = 2.16$, $0.2>P>0.1$).

Two detected alleles were unique to *P. elegans* and six to *P. adelaidae* (Table 2). None occurred at frequencies significantly higher than zero except $Pgm^a$ in the comparison of the Flinders Ranges *P. adelaidae* sample with all other samples of *P. adelaidae* pooled together.

Comparisons of Gene Frequencies

Even allowing for the small sizes of the samples, significant differences in gene frequency were few, especially between *P. elegans* and *P. flaveolus*. Atherton Tableland *P. elegans* despite its geographical isolation, differed significantly from *P. flaveolus* and the other *P. elegans* samples only in gene frequencies at the *Idh–1* locus. South-East *P. elegans* showed no significant differences from *P. flaveolus*. One significant difference between South-East and Kangaroo Island *P. elegans* was detected at *Np*. The six samples from Kangaroo Island all lacked the $Np^b$ and, as well, the $Pgd^c$ genes found in *P. flaveolus* and South-East *P. elegans* and also the $Idh\text{–}2^b$ gene found in *P. flaveolus* and *P. adelaidae*. Only for $Np^b$ in the Kangaroo Island *P. elegans-P. flaveolus* comparison was such a difference significant ($P = 0.043$).

$Pgd^a$ occurred at a significantly higher frequency in Kangaroo Island *P. elegans* than in *P. adelaidae* samples, S, Ma and F and all *P. adelaidae* samples pooled, and was greater also in *P. flaveolus* and sample M than sample

S. $Np^a$ occurred at a significantly greater frequency in Kangaroo Island *P. elegans* than in *P. adelaidae* samples Ma and C and all *P. adelaidae*.

Within *P. adelaidae*, significant differences in gene frequency were few and showed no consistent geographical pattern. The Flinders Ranges sample of *P. adelaidae* differed significantly from other *P. adelaidae* samples pooled only for *Pgm* ($0.05>P>0.02$).

Enzyme Expression

The enzyme products of *Idh–1* and *Acon–1* were strongest in liver extracts, while those of *Idh–2* and *Acon–2* were strongest in heart extracts. Avise *et al.* (1980) noted the same difference for *Idh* loci in North American thrushes and their allies. Wholly or largely invariant enzymes were both glucose- and non-glucose metabolizing.

## Discussion

Although breeding studies in rosellas have not been conducted to test the mode of inheritance of the proteins examined in this study, Mendelian inheritance has been assumed because:

(i) the proteins examined display Mendelian inheritance wherever studied in other organisms (see, for examples, Harris & Hopkinson 1976); and

(ii) population data satisfy Hardy-Weinberg expectations such as to render unlikely any other mode of inheritance approximating Mendelian expectations.

Thus, the isozymic data obtained in this study may be used to discuss genetic relationships and variation.

The sample sizes used in this study, particularly those of *P. elegans* and *P. flaveolus* were rather small. Baverstock *et al.* (1977) have shown nonetheless that such samples can be adequate to indicate relationships in electrophoretic studies, although they did not negate the desirability of having larger samples, especially for studies of within-population variation.

The genic variation measured in the rosellas, genically limited though it is, is consistent with evidence that levels of genic variation in birds are much the same as those in other vertebrates. Similarly, the paucity of genic differentiation between the rosellas may support the concept that in birds morphologically quite different taxa exhibit relatively less structural gene differentiation within an Order than do other animal groups. Consistent with this were the observations of alleles shared by the parrot genera *Barnardius*, *Psephotus* and *Platycercus*. Nevertheless one should note that although *P. elegans* and *P. flaveolus* appear quite different, there could be a simple genetic basis to their plumage differences. A full discussion of the concept of weak structural gene differentiation in birds is not intended here; the reader is referred to the reviews and alternative opinions presented by Sibley & Ahlquist (1982) and Avise & Aquadro (1982).

If sampling in *P. adelaidae* has been comprehensive, the evolutionary and genetic significance, if any, of 'unique' alleles in *P. adelaidae* shall remain obscure until more extensive samples of *P. elegans* and *P. flaveolus* are collected. Bearing in mind the possibility that *P. adelaidae* evolved by hybridization, we would note that the phenomenon of 'unique' alleles in hybrid populations has been observed previously and discussed by Golding and Strobeck (1983).

Some of the differences in gene frequency between Kangaroo Island *P. elegans* and other populations may be due to stochastic effects. This population has been isolated for some 10 000 years (Lampert 1979).

Four presumptive pyruvate kinase heterozygotes (double-banded) were detected in liver extracts of *P. adelaidae*. Heart extracts of three of these individuals were found to be single-banded. Possibly, pyruvate kinase is modified in the liver, producing a secondary band on gels, thereby creating a false impression of heterozygosity in homozygotes. Alternatively, a gene for pyruvate kinase may be 'switched-off' in the hearts of rosellas heterozygous for it. Extracts from other organs and analysis of data from parents and their offspring would resolve this anomaly. Almost certainly, this difference explains the statistical heterogeneity in the *P. adelaidae* data for pyruvate kinase.

Relationships in the *P. elegans* species-group

As noted above, Cain (1955) and Keast (1961) suggested that the members of the *P. elegans* complex evolved *in situ* in response to climatic changes. Alternatively, Ford (1977) proposed that *P. flaveolus* originated in the Mt Lofty Ranges while isolated from *P. elegans* by arid country in the region of the Coorong during an arid part of the Pleistocene. According to this interpretation, *P. flaveolus* moved northwards into the Flinders Ranges

and eastwards to the Murray-Darling system when this barrier broke down, while *P. elegans* moved westwards and freely hybridized with *P. flaveolus* in the Mt Lofty Ranges, producing *P. adelaidae*. Although Ford (1977) was able to suggest dates for these proposed events from geological data, one of his postulates, namely that of Flinders Ranges *P. adelaidae* being isolated by seventy kilometres from other populations of *P. adelaidae* to the south, appears to be exaggerated. Any 'isolation' of this population can be by no more than thirty to forty kilometres. Moreover, it is unlikely to be permanent owing to the vagility of rosellas combined with the existence of habitat corridors, and has undoubtedly been promoted by, if it is not entirely consequent upon, agricultural clearing of vegetation in the northern Mt Lofty Ranges within the last 100 years. Thus, given the likelihood of gene flow through all populations of *P. adelaidae*, the mechanism of the maintenance of clinal plumage variation in *P. adelaidae* remains problematic. Neither Hardy-Weinberg equilibria nor regression and correlation analyses suggested that strong selection differentials act on electrophoretic characters in *P. adelaidae*. The existence of some measure of selection is suggested by the clinal variation in plumage itself and by the *Pgm* and *Idh–2* gene frequency differences between the Flinders Range and other *P. adelaidae* samples.

Concerning the relationship between *P. flaveolus* and *P. adelaidae*, Short (1969) argued that it should be determined whether the two overlap with only some hybridization or with extensive hybridization: the former situation would indicate effective reproductive isolation, the latter conspecificity. Unfortunately, the observations and claims of Lendon (1973) and Condon (1969, 1975) concerning overlap between the two lack adequate supporting evidence. Present-day hybridization between them or, more specifically, introgression of *P. flaveolus* genes into *P. adelaidae* is suggested by the *Idh–2* data. $Idh–2^b$ was not detected in *P. elegans* but it was in *P. flaveolus* and several samples of *P. adelaidae*, including that taken from the Marne River region where *P. adelaidae* and *P. flaveolus* are perhaps closest (unpubl. data). More material would be useful in evaluating this and any other interpretations.

Overall, the genic data indicate a close relationship between the three rosellas studied but at present they are insufficient to determine with certainty whether the birds constitute a single biological species. There is scope for much further work on the group. The mechanism and maintenance of the clinal variation in, and the significance of 'unique' genes in *P. adelaidae* could be clarified with more extensive field and laboratory analyses. Also, the relationship of *P. caledonicus* to the other members of the complex warrants investigation as does a much closer examination of the genetic relationships between all the members. A karyotypic analysis may prove useful, specially to test further the hypothesis of a hybrid origin of *P. adelaidae*.

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